

Do ecosystems need top predators? A review of native predator-prey imbalances in south-east Australia

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Abstract

The role of native top predators in regulating terrestrial ecosystems in south-east Australia is briefly reviewed. Examples of ecological imbalance associated with overabundant native herbivores are identified. The cases of tree canopy loss due to excessive browsing by Koala and Common Ringtail Possum are discussed. The widespread loss of native top predators has left two introduced mesopredators, the Red Fox and Cat, to regulate both native and introduced herbivores in many areas. However, being ground-based predators, they are not efficient at controlling ringtail possums in dense vegetation, and without the top predator Dingo they may be ecologically released, increasing their impact on sensitive fauna. Management approaches to keeping a balance between predators and herbivores are outlined. (*The Victorian Naturalist* 132 (1), 2015, 4–11)

Keywords: predator; mesopredator; herbivore; owl; quoll; koala; possum; fox; cat; tree decline

Introduction

Many ecosystems are influenced or shaped by apex or top predators. Large carnivores can control populations of smaller mesopredators and herbivores, preventing them from monopolising or destroying resources needed for overall biodiversity (see Stolzenburg 2008).

This review explores whether top predators play or previously played a role in regulating terrestrial ecosystems in south-east Australia by controlling mesopredators and herbivores.

It is suggested that exotic mesopredators have partly replaced the original top predators and mesopredators, and despite their drawbacks they continue the necessary ecological function of herbivore control. Where herbivores, native or introduced, are not controlled top-down by predators, they may be bottom-up controlled by starvation, and ecosystems can collapse.

Original top predators and mesopredators of south-east Australia

The original (pre-European) major top terrestrial predators of south-east Australia are listed in Table 1. Table 2 lists the original major terrestrial mesopredators.

Perhaps the ultimate predators were humans. Through hunting and also by imposing fire regimes, Aborigines greatly influenced animal populations (Gammage 2011). In south-east Australia most animals, including marsupial herbivores, were hunted as a source of food and raw materials; cloaks were made from ani-

mal skins, notably those of brushtail possums. Aborigines may have preyed on dingoes as in Western Australia where the puppies were regarded as a delicacy, although they were sometimes reared by the Aborigines for hunting (Meagher 1974). Early Europeans were also major predators of marsupials.

Long gone are the Pleistocene giant top carnivores *Thylacoleo*, *Megalania* and *Wonambi* and many of their large prey such as *Diprotodon*. After the extinction of much of the megafauna and later arrival of the Dingo, south-east Australia had a simplified food web which was then further modified by the arrival of Europeans with their introduced predators and herbivores.

Present day predators

Most of the native top terrestrial predators and mesopredators of south-east Australia are extinct or their populations are mostly fragmented and reduced. The Dingo is still the top ground predator in remote eastern Victoria and adjacent NSW. However, due to persecution it is now absent from most of its former range. Arriving several thousand years ago, the Dingo may have replaced the Thylacine on the mainland. The Dog *Canis lupus familiaris* is widespread and feral dogs are subject to a government bounty.

Two introduced mesopredators are widespread and abundant in south-east Australia and in the effective absence of native top preda-

Table 1. Original major top predators of south-east Australia.

Common name	Species	Scientific name	Status (Victoria, based on DSE 2013)
Dingo (Fig. 1) (may be regarded as native)		<i>Canis lupus dingo</i>	Fragmented, data deficient
Thylacine		<i>Thylacinus cynocephalus</i>	Extinct
Wedge-tailed Eagle		<i>Aquila audax</i>	Widespread, secure
Peregrine Falcon		<i>Falco peregrinus</i>	Widespread, secure
Powerful Owl		<i>Ninox strenua</i>	Fragmented, vulnerable
Lace Monitor		<i>Varanus varius</i>	Fragmented, endangered

Table 2. Original major mesopredators of south-east Australia.

Common name	Species	Scientific name	Status (Victoria)
Spot-tailed Quoll		<i>Dasyurus maculatus</i>	Fragmented, endangered
Eastern Quoll		<i>Dasyurus viverrinus</i>	Regionally extinct (extant in Tasmania)
Western Quoll		<i>Dasyurus geoffroii</i>	Regionally extinct (extant in WA where threatened)
Tasmanian Devil (could be considered a top predator)		<i>Sarcophilus harrisi</i>	Restricted to Tasmania where threatened
Laughing Kookaburra		<i>Dacelo novaeguineae</i>	Widespread, secure

tors are surrogate top predators in some areas:

- Red Fox *Vulpes vulpes*
- Cat *Felis catus*

Neither predator is aerial or highly arboreal and so cannot replace local extinctions of these predator types, which changes the predator regime to being ground-based in affected areas.

Native herbivores that may become overabundant without predators

Under low predator pressure, several native herbivorous mammals may increase and become overabundant in areas of south-east Australia, that is, they cause an ecological imbalance leading to loss of species diversity (Table 3).

Case studies

Koala

Overabundant Koala populations impact on their habitat by overbrowsing preferred food tree species in a few coastal areas and some islands of Victoria including Mount Eccles, Framlingham Forest, the Otway Ranges (Fig. 2),

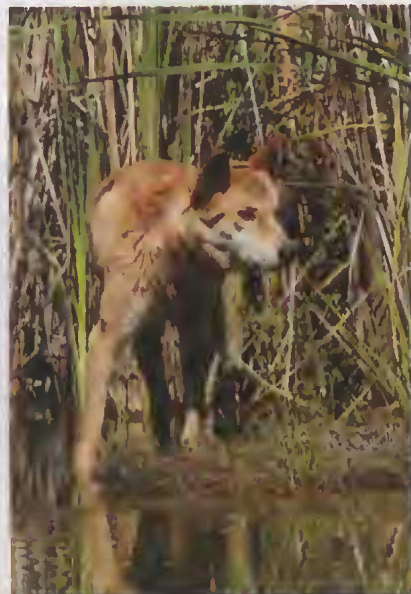


Fig. 1. Dingo. Photo by Peter Menkhorst.

Table 3. Native herbivores associated with ecological imbalance.

Species	Original major predators	Examples of ecological imbalance
Common Ringtail Possum <i>Pseudocheirus peregrinus</i>	Powerful Owl, Spot-tailed Quoll, Aborigines	Tree canopy loss on northern Mornington Peninsula
Common Brushtail Possum <i>Trichosurus vulpecula</i>	Thylacine, Dingo, Spot-tailed Quoll, Lace Monitor, Aborigines	Tree losses in River Red Gum woodland on fringes of Melbourne
Eastern Grey Kangaroo <i>Macropus giganteus</i>	Thylacine, Dingo, Aborigines	Overgrazing inside predator exclosures and by very high unrestrained populations in many locations in Victoria, especially on urban fringes
Western Grey Kangaroo <i>Macropus fuliginosus</i>	Dingo, Aborigines	Loss of plant diversity in Mallee national parks and reserves
Black Wallaby <i>Wallabia bicolor</i>	Dingo, Aborigines	Loss of plant diversity within predator exclosure, Royal Botanic Gardens Cranbourne
Koala <i>Phascolarctos cinereus</i>	Dingo, Aborigines	Tree canopy loss in several locations in Victoria
Swamp Rat <i>Rattus lutreolus</i>	Eastern Quoll, ?Aborigines	Widespread loss of orchid populations on Mornington Peninsula

French Island and Snake Island (Menkhorst 2008). Coast Manna Gum *Eucalyptus viminalis* subsp. *pryoriana* is particularly at risk, but Koalas also can impact on Swamp Gum *Eucalyptus ovata*, Southern Blue Gum *Eucalyptus globulus* and River Red Gum *Eucalyptus camaldulensis*.

The Koala overpopulation problem has been much studied (for example Martin 1985a,b; Menkhorst 2008; Todd *et al.* 2008; Wallis 2013). The Victorian government has moved away from translocation as a management technique and is now using in situ chemical sterilisation

to manage overabundant populations in several locations (Menkhorst 2004, 2008). Several factors control Koala populations, notably predators, road kill, fire, disease and food supply. There is evidence that predation by Aborigines and Dingoes kept Koala numbers very low prior to European settlement (Strahan and Martin 1982; Menkhorst 1995).

Possums

Common Ringtail Possum and Common Brushtail Possum are widespread primarily



Fig. 2. Southern Blue-gum forest defoliated by Koala overbrowsing, Kennett River, Otway Ranges. Photo by Peter Menkhorst.

folivorous mammals that feed on many eucalypt and other species. Tree canopy loss due to mammal overbrowsing was not described when the vegetation of Victoria was in its 'original and natural' condition (see Hateley 2010) and seems to have developed since European arrival. As early as the 1870s Aborigines at Framlingham in western Victoria were 'accusing' brush-tail possums of killing trees. 'The possums were no longer hunted and their numbers had risen ... Possums also benefited when dingoes were culled.' (Low 2002, p. 242).

Possums have been involved in tree canopy loss in many areas of suburban and rural Victoria (Yugovic 1999b; Low 2002). Curiously, *Eucalyptus viminalis* subsp. *pryoriana* (rough-barked form), a common tree in heathy woodland in southern Victoria, is relished by Koalas but avoided by possums (pers. obs.).

In Mount Eliza on the Mornington Peninsula an overpopulation of Common Ringtail Possum is responsible for an ongoing and unprecedented epidemic of eucalypt tree death. All indigenous eucalypts are susceptible but Swamp Gum *Eucalyptus ovata* and Narrow-leaf Peppermint *E. radiata* are preferred by possums and are defoliated and killed first. Repeated defoliation is required to kill a healthy tree. With up to 16 ringtail possums per hectare, this is the highest density of ringtail possum recorded in natural eucalypt dominated vegetation in Australia. Brushtail possums are at low density for a peri-urban environment. This is evidenced by detailed observations (Carr *et al.* 2014) and the recovery of trees following installation of possum bands (Yugovic 2013b)(Fig. 3).

Several factors control populations of ringtail possum including availability of shelter, density of understorey vegetation, predation (originally mainly by humans, dingoes, spot-tailed quolls, large raptors and large owls, and now mainly by cats, foxes, large raptors and large owls where they occur), fire, food quality and availability, and heat waves. Ringtails have high fecundity (Kerle 2001) so populations can rapidly reach habitat carrying capacity.



Fig. 3. Possum band or guard on Swamp Gum *Eucalyptus ovata*, Mount Eliza. Clear plastic band on trunk (lower centre) protects tree crown from possums while unprotected side limb (on right) has died. Before installation of guard the entire tree was largely defoliated. Recovery took 6–12 months.

Both possums have higher densities in Melbourne's urban bushland due to increased food resources in adjacent residential areas (Harper *et al.* 2008), which may contribute to high browsing pressure in Mount Eliza, but possum-induced tree decline occurs across the rural northern Mornington Peninsula from Mount Martha to Cranbourne and was locally severe in the 1990s (Yugovic 1999a) before it became severe in urban areas in the 2010s. (Fig. 4) In Mount Eliza entire canopies are now dead or declining, and the 'prognosis for the eucalypts remaining in the landscape is extremely poor' (Carr *et al.* 2014, p. 42).

Possum-induced tree decline is not confined to the Mornington Peninsula as it occurs elsewhere in southern Victoria, for example at Braeside and Mordialloc.

Described locally as an 'ecological emergency', possum overbrowsing and occasional tree losses were occurring in Mount Eliza as early as the 1980s (pers. obs.). This continued through the Millennium Drought (1996–2010) and first became severe (with complete canopy losses) during the 2010–2012 La Niña event suggesting that high rainfall may favour possums. However there were many previous La Niñas before the drought (Bureau



Fig. 4. Distribution of possum-induced tree decline, northern Mornington Peninsula. Each affected site has 10 or more possum-affected dead or dying closely adjacent trees. Tree decline is not restricted to these sites as extensive areas are also affected between sites.

of Meteorology, Mornington weather station) and none caused complete canopy loss.

Could a predator-prey imbalance between domestic cats and ringtail possums help explain the late onset of the decline in Mount Eliza? With the native predators long gone, domestic cats were at artificially high densities as they were being fed and sheltered by their owners and were the last remaining major predators until 1997 when they largely disappeared from the landscape due to local control policies and programs including a cat curfew. However, given the possum overpopulation developed some 15 years after the cat curfew was introduced, it seems that some factor(s) other than, or in addition to, lack of cats has caused the increase.

Biomass accumulation is a necessary condition for ringtail possum overpopulation. Biomass builds up in a more-or-less continuous mid-storey or sub-canopy layer in the vegetation composed of shrubs and small non-eucalypt trees, which can be either indigenous or introduced. The possums construct their dreys in these dense shrubby understoreys and can avoid travel across the ground between food trees where they are vulnerable to ground predators. Dense, unburnt understoreys are prevalent on the northern Mornington Peninsula.

In addition to bushland remnants, street and

garden trees in Mount Eliza with dense understoreys are also severely affected by ringtail possum overbrowsing (Carr *et al.* 2014). In the general absence of biomass reduction, there has been a general increase in understorey biomass on road reserves and in adjacent gardens over time, particularly with the 2010–2012 extended La Niña event stimulating growth of both eucalypts and understorey.

The grassy woodlands of the northern Mornington Peninsula were once much more open than the bushland remnants and gardens of today as evidenced by annotations on historical survey plans. This was likely due to Aboriginal burning and macropod grazing and browsing (Yugovic 2013a). It follows that ringtail habitat carrying capacity was limited at that time which would have assisted in keeping woodland canopies healthy. The carrying capacity is higher now with the mostly dense unburnt and ungrazed understoreys — until the canopy dies.

The Mornington Peninsula tree decline phenomenon appears to be a syndrome of (1) susceptible eucalypts, (2) high biomass accumulation and (3) low predator pressure leading to (4) ringtail possum overpopulation. Low predator pressure appears to be a necessary condition — if there was high predator pressure there would be no possum overpopulation. However, this

assumes the original full suite of aerial, arboreal and ground predators could control ringtail possums in dense vegetation, and is therefore speculative. The lack of early reports of possum-induced tree decline in Victoria and reports of dense understoreys in many areas at the time (Hateley 2010) suggest that they could.

Two key native predators are locally extinct: Powerful Owls took possums from tree canopies while Spot-tailed Quolls took possums from within trees. The latter have extraordinary speed and agility in trees, having adaptations on their feet for climbing: presence of a first toe, and serrated pads on the palm and sole (Troughton 1957). Aerial and arboreal predators, native or introduced, are effectively missing from the current predator regime.

Furthermore, many areas elsewhere in south-east Australia including sites supporting Swamp Gum currently have dense understoreys and native and introduced predators (Victorian Biodiversity Atlas, data) with ringtail possums and tree canopies apparently in balance.

Certainly the best management response on the Mornington Peninsula now is to reopen understoreys as culling of possums and reintroducing predators are impractical. This also has benefits for ground layer flora diversity, which slowly declines under shady scrub.

In the Melbourne region, however, large River Red Gums *Eucalyptus camaldulensis* with open grassy understoreys have been killed by brush-tail possums that den in natural hollows. Dense understoreys are not needed by the less arboreal (scansorial) brushtails.

Discussion

It is widely accepted that introduced predators threaten many native species in south-east Australia, particularly mammals (e.g. Dickman 1996), but how does predator pressure differ now from originally? Often a predisposing problem underlying local extinction is isolation of habitat, which is either natural or more usually is caused by land clearing and disturbance. Would the original suite of predators cause the same local extinctions if they were still present? These and similar questions of predator ecology need further research.

Based on extensive observations, it appears that in some areas the introduced predators are not,

or are not capable of, keeping up with key native and introduced herbivores (such as rabbits) which are overabundant and causing ecological damage. Depending on the situation, low predation rates are partly due to predator inefficiency (for example the fox and cat have low efficiency with ringtail possum in dense mid-storey vegetation), and partly due to control which may in some cases leave some areas effectively without predators.

For example, Mount Eliza has bushland reserves where there are no threatened species and possums and swamp rats are the only native mammals apart from bats and occasional sugar gliders, and where cats are largely absent due to the local cat curfew. Foxes and cats are also actively controlled. These effectively predator-free areas are undergoing eucalypt canopy loss caused by possums, and orchid colony losses caused by swamp rats (Yugovic 2013b). In these novel ecosystems removing all predators is questionable when possums are killing the canopy trees along with dependent species including sugar glider, and orchids are going locally extinct.

Systems without top predators are likely to undergo trophic imbalance with adverse ecological cascade effects on flora and fauna (see Stolzenberg 2008). Whether the predators or prey are native or introduced during trophic imbalance seems to make little difference to overall biodiversity — overabundant herbivores, native or introduced, inevitably degrade ecosystems. Current land management is pushing systems towards domination by browsing and grazing mammals, with other influences such as predation and regular fire being reduced.

A feature of the introduced mesopredators is their apparently higher predation rates on certain native species compared to the original suite of predators, for example the fox appears to have eliminated the Tasmanian Pademelon on mainland Australia. This increased predation may be related to particular efficiencies in new predator-prey relationships, but may also be related to 'mesopredator release' (Crooks and Soulé 1999). Mesopredator release is thought to operate extensively in Australia in areas where the top predator Dingo is rare or absent, resulting in higher mesopredator populations and predation rates (Johnson *et al.* 2007).

Outside the 5600 km arid zone dingo fence, for example, dingoes appear to suppress fox populations and thereby assist small to medium native mammals (Letnic *et al.* 2009). Similarly, there is evidence from south-east Australia that dingoes suppress numbers of macropods and foxes and thus generate strong indirect and beneficial effects on the prey of foxes (Letnic *et al.* 2009). This suggests that mesopredator release of the fox operates extensively in south-east Australia where dingoes are absent, to the detriment of small and medium mammals.

An interesting predator manipulation experiment in semi-arid WA found that when dingoes and foxes were both removed cats increased and predation on small mammals increased further (Risbey *et al.* 2000), suggesting a hierarchy of predators (dingo, fox, cat) and ecological release processes. As the authors acknowledge, this needs replication. The evidence for an increase in cat abundance following fox control is inconsistent between studies, and there is also limited knowledge on the impacts of feral cats and foxes on native predators (Robley *et al.* 2004). Interactions between predators such as aggression, competition for prey and predation on juveniles need further research.

According to proponents, 'rewilding' with apex predators has benefits for ecosystem stability and diversity (e.g. Soulé and Nos 1998; Monbiot 2013). The predators are either regionally extinct or are related to extinct Pleistocene predators. For example Komodo dragon could replace *Megalania* in order to control feral water buffalo in northern Australia (Flannery 1994; Bowman 2012). However, many people would find it unacceptable to replace extinct marsupial predators with placental predators such as large cats in south-east Australia, although they could provide a means of controlling populations of feral pigs, horses and deer.

Flannery (1994) also proposes reintroducing the long extinct Tasmanian Devil to mainland Australia where it could play a role in checking foxes and cats. Devils are thought to enter fox dens and eat the cubs (DSEWPac 2012), which may explain why attempts to introduce the fox to Tasmania have not been successful. Devils also prey on possums. There have been moves to reintroduce devils to Wilsons Promontory but no program has been formalised.

Conclusion

Many ecosystems in south-east Australia appear to benefit from or require top predators in maintaining stability and complexity as do ecosystems elsewhere (see Stolzenburg 2008). Whether the introduced mesopredators have any net benefits is doubtful given their high toll on sensitive fauna but they do carry on the necessary function of herbivore control.

Unlike North America and Europe where top predators such as wolves, lynx, cougars, jaguars and bears are being returned to ecosystems with beneficial effects, the return of the dingo is impractical in much of Victoria as it can prey on livestock and may interbreed with domestic dogs to produce packs of wild dogs. The dingo survives in remote eastern Victoria, however.

Due to the widespread loss of native top predators and mesopredators, in many areas we are left with two introduced mesopredators (the fox and cat) to control herbivores. However, being ground-based predators they are not efficient at controlling ringtail possums in dense understorey vegetation. Furthermore, without the top predator dingo they appear to be ecologically released, increasing their impact on sensitive fauna.

Possible management approaches to maintaining a balance between predators and herbivores in south-east Australia include the following:

- Land managers should be aware of the complexities of predator ecology and feral animal control, and should anticipate and look for ecosystem responses including changes in herbivore pressure on vegetation.
- Predator control should be undertaken strategically where identified significant fauna are under identified predator threat, in combination with monitoring of canopy health, sensitive plant populations and other ecological indicators.
- Where necessary, large trees should be protected from mammal folivores, especially in prominent locations. This is happening in Mount Eliza with the Mornington Peninsula Shire installing possum hands on trees on roadsides and in reserves, with good results.
- Due to their potential detrimental effect on canopy trees, constructed nest boxes for brushtail and ringtail possums are

often not appropriate. Release of rescued or trapped possums into bushland should not be undertaken where habitats are already at carrying capacity for possums. The protected status of these species in areas with possum-induced tree decline should be reviewed in order to protect trees and biodiversity.

- Managing woodlands towards their original open structure through biomass reduction counters the impact of ringtail possums by reducing habitat carrying capacity.
- We should redouble our efforts to protect all native apex predators in order to allow these keystone species to perform their important ecological role of controlling herbivore pressure within natural areas.

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